

THE GENERA OF RHAMNACEAE IN THE
SOUTHEASTERN UNITED STATES ¹

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RHAMNACEAE A. L. de Jussieu, Gen. Pl. 376. 1789, "Rhamni," nom. cons.
(BUCKTHORN FAMILY.)

Deciduous or evergreen trees, shrubs, or woody vines [exceptionally herbs], unarmed or armed with thorns or stipular spines. Leaves simple, alternate, subopposite, or opposite, petiolate; stipules mostly free, more rarely connate across the axil, usually minute and caducous, sometimes modified to spines [rarely absent]. Inflorescences axillary few-flowered umbel- or corymb-like cymes (sometimes reduced to a solitary flower), or axillary and/or terminal raceme- or spikelike thyrses. Flowers small or minute, regular, perigynous to epigynous, with a distinct floral tube, bi- and/or unisexual by abortion, pediceled or sessile. Floral tube ("hypanthium") patelliform to hemispherical or campanulate [or urceolate to cylindrical], persistent in fruit at least in part; calyx lobes usually 4 or 5, valvate in aestivation, usually deciduous either separately or with the sometimes circumscissile upper part of the floral tube, rarely persistent. Petals 4 or 5, alternate with the calyx lobes, \pm concave or hooded or flat, often clawed, enfolding the stamens in aestivation, or wanting. Stamens 4 or 5, opposite the petals, adnate to them at the base and inserted at or below the margin of the disc, smaller and sterile in $\text{\textit{f}}$ flowers; filaments usually subulate, longer or sometimes slightly shorter than the anthers; anthers dorsifixed, usually nonversatile, 2-locular at anthesis, longitudinally dehiscent; pollen usually 3-colporate, suboblate to subprolate, small to medium sized, often \pm triangular in polar view, \pm smooth to reticulate. Nectariferous disc intrastaminal, hypogynous to epigynous [rarely wanting]. Gynoecium 2- or 3[4]-carpellate, syncarpous, rudimentary in $\text{\textit{m}}$

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flowers; stigmata 2 or 3 [4] or stigma 1, usually lobed; style 1, often 2- or 3 [4]-lobed to -parted; ovary 2- or 3 [4]-locular, sometimes incompletely so at the very base [or in the middle, or rarely throughout], the septation diverse; ovules solitary [exceptionally 2] in each locule, basal [or sub-basal?], ascendent, anatropous, epitropous or (more commonly) pleurotropic (the raphe lateral) [very rarely apotropous?], 2-integumented, with a thick nucellus, funiculate. Fruit usually a drupe with 2 or 3 [4] dehiscent or indehiscent pyrenes, or with a (1-) 2- or 3-locular dehiscent or indehiscent stone, or rarely a commissurally winged [or unwinged] schizocarp, with [or without] a carpophore.² Seed convex and smooth or rarely grooved on the back (abaxial side), with lateral, rarely dorsal, raphe, sometimes minutely [or conspicuously] arillate; endosperm scanty or copious, rarely ruminant, or wanting; embryo "investing," usually large, axial, straight; cotyledons flat or plano-convex; radicle inferior. TYPE GENUS: *Rhamnus* L.

A family of nearly 55 genera and 900 species, of the Tropical and Temperate zones of both hemispheres, the northern limit of the range mostly running between 50° and 55° N. Lat. Five tribes generally are recognized. Intergeneric relationships show many reticulations, and it is likely that further studies will result in a reduction in the number of genera.

The small, generally inconspicuous flowers, which always have a floral tube formed by the fusion of basal parts of the perianth and androecium, are mostly bisexual. Unisexual flowers, with consequent polygamy and/or mono- or dioecism, occur within some genera (e.g., *Berchemia*, *Gouania*, *Rhamnus* spp.) but only rarely, if at all, are a character of generic significance. Cross-pollination by hymenopterous, coleopterous, and dipterous insects seems to be the rule, but data are available for relatively few genera and species. Pollen morphology is relatively uniform throughout the family.

² Fruits in Rhamnaceae have often been characterized as drupes and/or berries and/or capsules. Recently, Vikhireva, on the basis of the gross morphology and histology of the fruits of this family, classified them as syncarpous drupes throughout. Such drupes are in many cases, perhaps in most, closely related to capsules, on the one side, and to schizocarps, on the other, being a link of an evolutionary sequence from syncarpous capsule to syncarpous drupe to schizocarp (*sensu stricto*). It is not surprising, therefore, that among the syncarpous drupes of Rhamnaceae there are forms not only similar to but apparently intermediate to capsules and schizocarps. The classification of forms intermediate to schizocarps seems to be especially difficult, at least in some cases. In this respect, Rusby's suggestion (in Rusby & Jelliffe, *Morphology and Histology of Plants*, pp. 110, 111. 1899) can be helpful. Since schizocarps are commonly provided with appendages for transportation by wind or by mechanical adhesion to passing bodies, "those forms which as above stated are intermediate toward drupes are to be classed in one or the other class, according to whether such appendages for distribution, or that of edible [\pm fleshy] pericarp [mesocarp], is the more pronounced." In concurrence with both this suggestion and Vikhireva's conclusions, the fruits of Rhamnaceae are classified here as drupes, except those in *Gouania* and its allies, which are regarded as schizocarps.

The structure of the ovary with regard to the number of carpels, the mode of septation ("placentation"), and the fertility or sterility of the septal margins representing the margins of two adjoining connate carpels seems to be a character important for understanding the evolution of the family (see Suessenguth, pp. 31-33). As a rule, only one of the two margins of a carpel forming an ovary locule is fertile, and the sequence of the fertile and sterile margins of carpels or septa in a three-locular ovary can be different in different genera. Consequently, two general situations are possible: in the first case, one of the septa is fertile on both its margins, the second on one, and the third completely sterile (e.g., *Rhamnus* spp.); in the second case, each septum is fertile on one of its margins (e.g., *Ceanothus* spp.).

Basal placentation has generally been regarded as one of the most distinctive features of Rhamnaceae. Prichard confirmed this for at least six genera which he investigated and also remarked, "The ovules do, however, develop from the lateral [slightly incurved] margins of carpels" (p. 103). This agrees with the explanation offered by Suessenguth (*loc. cit.*) and seems to make it rather clear that this basal placentation is one of the variants of axile placentation, or at most a derivative of it. (See, however, Nair & Sarma, p. 54).

Chromosome counts made for eleven genera (55 species) are $2n = 18, 20, 22, 24, 26, 34, 36, 37, 40, 48, 49,$ or $50, 72,$ and $96,$ suggesting that both aneuploidy and polyploidy have been of importance in the evolutionary development of Rhamnaceae. It is notable that $2n = 24$ is the most frequent chromosome number occurring in at least some species of eight genera, and that both highly polyploid and homoploid genera occur in the family.

In most of our genera the seeds are dispersed mainly by birds and mammals (e.g., *Rhamnus*, *Berchemia*, *Reynosa*, *Sageretia*, *Krugiodendron*), rarely by wind (e.g., *Gouania*) or by water (*Colubrina asiatica*). In some, the fruits themselves are mechanically active ("explosive fruits"), ejecting seeds short distances (e.g., *Ceanothus*, *Colubrina* spp.).

A close relationship of Rhamnaceae to Vitaceae seems to be unquestionable. The relationship to Celastraceae presumed by Prichard and some taxonomists (cf. Suessenguth) is denied by Nair & Sarma (p. 54), who remarked, "It must be noted that floral-anatomically there is very little in common between the two families (see Berkeley, 1953). Further the embryological and palynological data do not support any relationship between the two families. . . ."

Species of several native and exotic genera (e.g., *Paliurus*, *Pomaderris*, *Colletia*) are cultivated as ornamentals. The eastern Asiatic *Hovenia dulcis* Thunb., raisin tree, $2n = 24$, cultivated as an ornamental and for its fleshy, edible rachis and inflorescence branches, has been recorded as escaped and spreading very slowly in Polk County, North Carolina (Freeman). Some species yield wood of local importance (e.g., the tropical African *Maesopsis Eminii* Engl., musizi; the East African *Phyllogeiton Zeyheri* (Sond.) Suesseng., pink or red ivory wood). Fruits, bark, and/or roots of some species are sources of drugs or natural dyes.

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KEY TO THE GENERA OF RHAMNACEAE

General characters: *woody plants; flowers small, regular, 4- or 5-merous, bisexual, more rarely unisexual; floral tube always developed; petals mostly concave or hooded, often unguiculate, or wanting; stamens 4 or 5, opposite the petals; nectariferous disc intrastaminal; gynoecium syncarpous, the ovary superior to inferior, 2- or 3-locular; ovule solitary in each locule, basal, ascendent; fruit a syncarpous drupe or a schizocarp.*

A. Leaves alternate.

B. Plants climbing by twining or by tendrils.

C. Vines climbing by twining; leaves entire, with 9-12 pairs of straightish subparallel veins; ovary superior, 2-locular; fruit a bluish-black ellipsoid to obovoid 1-stoned drupe. 5. *Berchemia*.

C. Vines climbing by solitary tendrils near base of peduncle of inflorescence; leaves coarsely and remotely crenate-serrate, with 4-7 pairs of curved, somewhat convergent lateral veins; ovary inferior, 3-

locular; fruit a 3-winged schizocarp ca. 1 cm. broad, splitting along each wing into three 2-winged mericarps. 9. *Gouania*.

B. Plants erect shrubs or trees.

D. Inflorescences dichotomously branched manifestly peduncled many-flowered axillary and terminal thyrses, the branches becoming club shaped, fleshy, and reddish in fruit; nectariferous disc pubescent; drupe leathery, subglobular, light grayish or brownish, with a thin-coriaceous, indehiscent, 3-locular stone; leaves large, 3-nerved at base, the petiole 2.5–4 cm. long; deciduous ornamental tree sparingly escaped from cultivation. [*Hovenia* Thunb.]

D. Inflorescences neither dichotomous nor fleshy in fruit; nectariferous disc glabrous; petiole usually short.

E. Drupe fleshy, superior, subtended at base by a flat remnant of the floral tube; inflorescences few-flowered corymb- or umbel-like fascicles, short peduncled to sessile.

F. Branchlets bearing flowers and fruits often fascicled in axils of leaves or leaf scars, usually deciduous; stipules modified to spines; petals hooded, conspicuously clawed; nectariferous disc flat, \pm pentagonal, encircling the ovary up to a conspicuous stylopodium; drupe red to brown or black, ellipsoid; stone solitary, hard, sharp pointed, indehiscent; leaves 3-nerved almost to the apex, lateral veins often obscure; cultivated and naturalized deciduous shrub or small tree. 6. *Ziziphus*.

F. Branchlets not fascicled; stipules caducous; nectariferous disc lining walls of floral tube, free from ovary; stylopodium absent; drupe nearly black, subglobular to almost obovoid, with 3 distinct dehiscent or indehiscent pyrenes; leaves pinnately veined, finely serrulate. 1. *Rhamnus*.

E. Drupe leathery, semi-inferior, adnate to a cuplike floral tube either at base or to half its length, separating into 3 dehiscent pyrenes or pyrene-like carpels; disc \pm annular, encircling the semi-inferior ovary; inflorescences many- to few-flowered thyrses.

G. Inflorescences usually many-flowered corymb- or raceme-like axillary or terminal thyrses longer than the subtending leaves; calyces and elongated filiform pedicels white; petals white, long clawed, much longer than the calyx lobes; leaves usually toothed, 3-nerved at least at base; drupes subglobular or obovoid, distinctly 3-lobed; deciduous low shrubs or subshrubs. 3. *Ceanothus*.

G. Inflorescences few-flowered contracted axillary thyrses much shorter than the subtending leaves; calyces and pedicels green; petals yellow to greenish or white, very short clawed to sessile, as long as or shorter than the calyx lobes; leaves pinnately nerved and entire or 3-nerved at base and/or serrulate; drupes subglobular, inconspicuously 3-lobed or unlobed; evergreen shrubs or small trees; southernmost Florida. . . . 4. *Colubrina*.

A. Leaves opposite and subopposite.

H. Leaves usually acute or short-acuminate at apex, serrulate or serrulate-crenate, ovate; stipules free, caducous; flowers petaliferous, sessile, in slender, spikelike, often paniced axillary and terminal thyrses much longer than the subtending leaves; drupe containing (2) 3 distinct,

- flattish, dehiscent pyrenes; small spinescent shrub, occasionally clambering; southeastern Coastal Plain. 2. *Sageretia*.
- H. Leaves obtuse or rounded, usually notched at apex, otherwise entire; stipules \pm connate across the axil, persistent; flowers apetalous, pediceled, in few-flowered axillary cymes much shorter than the subtending leaves or sometimes solitary; drupe subglobular, with a single hard stone; southernmost Florida.
- I. Leaves thin-coriaceous, not revolute at margin, ovate to broadly elliptic, obtuse to rounded at base, with 4–6 pairs of conspicuous, slightly curved lateral veins and coarsely reticulated veinlets; stipules connate only at the very base; calyx lobes crested inside. 8. *Krugiodendron*.
- I. Leaves stiff-coriaceous, revolute at margins, oblong or oblong-elliptic to narrowly obovate, cuneate to rounded at base, with 6–15 pairs of straightish, usually obscure lateral veins and numerous finely reticulated veinlets (lens!); stipules connate at least half their length; calyx lobes crestless inside. 7. *Reynosa*.

Tribe RHAMNEAE

1. *Rhamnus* Linnaeus, Sp. Pl. 1: 193. 1753; Gen. Pl. ed. 5. 89. 1754.

Deciduous [or evergreen] unarmed [or armed] shrubs or trees [rarely woody vines] with scaly or naked buds. Leaves alternate [to opposite], membranaceous [to coriaceous], pinnately veined, toothed [or entire]. Inflorescences axillary sessile or peduncled umbel-like cymes, sometimes reduced to solitary flowers [or axillary and/or terminal thyrses or rarely racemes]. Flowers small, perigynous, pediceled, bisexual and/or unisexual by abortion, the plants then usually (polygamo-) dioecious. Floral tube \pm campanulate [to urceolate]; calyx lobes 4 or 5, greenish or greenish yellow, deciduous separately or with the circumscissile upper part of the floral tube after anthesis. Petals 4 or 5, shorter than calyx lobes, yellowish or whitish, usually broad, nearly ovate or obovate [or sometimes linear to filamentous], emarginate to bilobed at apex [rarely acute], often somewhat different in δ and φ flowers, usually short clawed, concave to flat [or hooded], inserted at upper margin of disc, or wanting. Stamens 4 or 5, as long as or somewhat longer than petals, sterile and \pm rudimentary [or wanting] in φ flowers; filaments slightly longer or shorter than anthers; anthers oblong-ovate to ovate in outline, \pm cordate at base, sometimes apiculate at apex. Nectariferous disc lining wall of floral tube, thin below, somewhat thickened above. Stigma 3-lobed or stigmata 2–3 and subcapitate-discoid; style simple or 2- or 3[4]-forked; ovary superior, 2- or 3[4]-locular, incompletely so at the very base; ovules epitropous or pleurotropous. Fruit a small subglobular to obovoid, usually black [or dark red, rarely yellow] drupe, with 2 or 3 [4] pyrenes; mesocarp fleshy, with tanniferous idioblasts or mucilage cavities; pyrenes cartilaginous to somewhat woody, \pm convex on abaxial (dorsal), somewhat angular to almost flat on adaxial (ventral) surface, with a distinct adaxial suture, dehiscent or indehiscent. Seed narrowly or broadly obovate to subor-

bicular, plano-convex or lenticular, smooth or longitudinally grooved on abaxial side; seed coat membranaceous, sometimes very thin and closely adherent [or adnate] to endocarp; endosperm fleshy, scanty; embryo large, the cotyledons curved or flat, the radicle short. Germination epigeal or hypogeal. (Including *Frangula* Mill.) LECTOTYPE SPECIES: *R. cathartica* L.; typified by S. F. Gray, Nat. Arrang. Brit. Pl. 2: 621. 1824, who included only this species in sect. *Rhamnus*. (Name from Greek, *rhamnos*, an ancient name of some species of the genus.) — BUCKTHORN.

A genus of 150 (or fewer) species, distributed primarily in the Temperate and Tropical zones of both hemispheres, abundant in eastern Asia and southwestern North America, scarce in Europe and Africa, absent from Madagascar, Australia, Polynesia, and southern South America; three indigenous species in our area.

The four subgenera exhibit reticulate relationships. The most distinctive differences are in the structure of pyrenes and seeds; in this respect subg. PSEUDOFRANGULA³ is intermediate between subgenera RHAMNUS and FRANGULA (cf. Wolf, pp. 18, 32). Subgenus SCIADOPHILA (Philippi) Benth. & Hook. (including only the Chilean *Rhamnus diffusa* Clos [*Colletia maytenoides* Griseb., *Sciadophila maytenoides* (Griseb.) Philippi]) is poorly known, especially in regard to the structure of pyrenes and seeds, and perhaps represents a distinct, but closely related, genus.

Subgenus RHAMNUS. Winter buds scaly; leaves alternate [to opposite]; flowers usually petaliferous and 4-merous, mostly bi- and/or unisexual; style forked; pyrenes usually dehiscent along the adaxial suture; seeds deeply grooved on the back, with an abaxial raphe on the bottom of the groove; cotyledons thin, curved around the intruded groove; germination epigeal. About 100 species, centered in eastern Asia, a few in Europe and in tropical Africa (exclusive of Madagascar), several in North America. *Rhamnus lanceolata* Pursh, a tall unarmed shrub, with lanceolate leaves and two-carpellate gynoecia, occurs on open wooded slopes, thickets, and glades, usually on calcareous soil, from Alabama and Tennessee west to eastern Texas and Arkansas, north to Nebraska, southern Iowa, southern Wisconsin, Indiana, southern Ohio, south-central Pennsylvania, West Virginia and Virginia. In the western part of the range var. *lanceolata*, with the leaves short-pubescent on the lower surface, seems to predominate, while in the eastern and southeastern part var. *glabrata* Gleason, with the leaves glabrous or promptly glabrate, appears to prevail. The status of these variants needs further study. The European *R. cathartica* L., common buckthorn, $2n = 24$, a spinescent shrub or small tree with 3- or 4-carpellate gynoecia, has become naturalized in Canada and from the Northeastern States south to Virginia.

Subgenus PSEUDOFRANGULA (Grubov) Brizicky. Winter buds scaly; leaves alternate; flowers apetalous, (4)5-merous, bi- and/or unisexual;

³ *Rhamnus* L. subg. *Pseudofrangula* (Grubov) Brizicky, stat. nov. *Rhamnus* L. sect. *Pseudofrangula* Grubov, Not. Syst. Leningrad 12: 125. 1950. TYPE SPECIES: *R. alnifolia* L'Hér.

style forked; pyrenes indehiscent; seeds not grooved, the raphe abaxial; cotyledons thin, \pm plane; germination epigeal. Four species, one North American and three eastern Asiatic. *Rhamnus alnifolia* L'Hér., a low shrub with 3-carpellate gynoecia, occurs in swamps, low woods, and meadows, often on calcareous soil, from Newfoundland to north-central Alberta, British Columbia, and Washington, south to central California and north-eastern Oregon, Idaho, Wyoming, Nebraska, Iowa to New Jersey, and West Virginia. It was formerly known from Cedar Creek, Campbell County, Tennessee, but this locality is now covered by Norris Lake. *Rhamnus Ishidae* Miyabe & Kudo, apparently closely related to our species, is endemic on Hokkaido, Japan; *R. Arnottiana* Gardner is endemic in Ceylon; and *R. purpurea* Edgew. is known from the Himalaya and adjacent China. The few species and their present distribution suggest the antiquity of this group.

Subgenus FRANGULA (Mill.) Reichenb. Winter buds naked; leaves alternate; flowers petaliferous, 5-merous, bisexual; style simple; pyrenes indehiscent; seeds not grooved, the raphe lateral; cotyledons plane, thickish; germination hypogeal. About 40 species, primarily American (26 species), centered in California and Mexico, occurring southward to Peru and Brazil, with one species in the West Indies; the remaining species mostly in eastern Asia, a few in Europe, North Africa, and the Azores. *Rhamnus caroliniana* Walt., Indian cherry, $2n = 24$, a shrub or small tree, the gynoecia 3-carpellate, occurs in low woodland in valleys along streams, on rocky open wooded slopes, upland ridges, thickets, and glades, commonly on limestone outcroppings, from Florida (Charlotte County on the west and Orange County on the east coast) to westernmost Texas, north to western Virginia, West Virginia, Ohio, Indiana, Illinois, and Nebraska. Two variants which occur throughout this range (although one may be prevalent locally) have sometimes been recognized as var. *caroliniana*, with the leaves glabrous or glabrescent beneath, and var. *mollis* Fern., with the leaves permanently pubescent ("velvety") on the lower surface. *Rhamnus caroliniana* is closely related to *R. betulifolia* Greene, of the southwestern United States and Mexico; both "are interpreted as derivatives of a stock which migrated from farther south and which also probably gave rise to such a species as *R. Purshiana* DC., now distributed from northern California to Washington" (McVaugh). The European *R. Frangula* L., alder-buckthorn, $2n = 20, 22, 26$, a shrub or small tree, the gynoecia 2-carpellate, has become naturalized at least in the Northeastern States, south to New Jersey.

Subgenus FRANGULA differs from our other subgenera in the mucilaginous walls of the epidermal cells and the presence of mucilage ducts in the collenchyma of veins of the leaves and in the fruits; in the uniseriate, several-celled hairs (as against unicellular); and in the somewhat different wood anatomy (cf. Record). On these bases the subgenus is often segregated (especially in Europe) as a distinct genus, *Frangula* Mill. Since, however, *Rhamnus* as a whole seems to have been inadequately studied,

especially with regard to its tropical members, generic segregation appears to be somewhat premature.

The genus is poorly known in regard to its biology, floral morphology, and anatomy. The bisexual flowers of *R. Frangula* have been recorded as proterandrous. Chromosome counts have been made for seven species. Four species of subg. RHAMNUS have $2n = 24$, and one (the tropical African *R. prinoides* L'Hér.), $2n = 34$; two species of subg. FRANGULA have $2n = 24$ and $2n = 20, 22, 26$. Two different forms of karyotype not corresponding to the subgeneric divisions have been found (cf. Dolcher). Fruit dispersal is mostly by birds.

The genus is closely allied to *Sageretia* Brongn.

A number of species are grown as ornamentals and/or hedge plants (e.g., *Rhamnus cathartica*, *R. Frangula*, *R. Purshiana*), and some yield wood of local importance (e.g., *R. Frangula*, *R. cathartica*) or drugs (*R. Purshiana*, *R. Frangula*, *R. cathartica*). *Rhamnus caroliniana* and *R. lanceolata*, as well as several species of the Pacific States (e.g., *R. californica* Eschsch., *R. Purshiana*) are important honey plants. Fruits of *R. alnifolia* are said to be poisonous. At least *R. alnifolia*, *R. cathartica*, *R. Frangula*, and *R. lanceolata* are known to be the alternate host for *Puccinia coronata* Corda, crown rust of oats.

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2. *Sageretia* Brongniart, Mém. Fam. Rhamn. 52. 1826.

Evergreen [or deciduous] spinescent [or unarmed] shrubs [or small trees]. Leaves opposite or subopposite, small [to rather large], thin-coriaceous [rarely coriaceous], pinnately veined, with 3–5 (6) pairs of

primary veins, serrulate [or entire]. Inflorescences terminal and axillary interrupted spikelike [very rarely raceme-like] often paniced thyrses [or the flowers glomerulate to solitary in leaf axils]. Flowers minute, 5-merous, bisexual, sessile [or very rarely pediceled], 2-bracteolate at base. Floral tube short-campanulate to patelliform [or hemispherical to urceolate (?)]; calyx lobes somewhat fleshy, keeled medially on inner surface, deciduous. Petals whitish, obovate, concave [or cucullate], minutely apiculate and often notched at apex, obscurely [or distinctly] unguiculate, much shorter than calyx lobes. Stamens slightly longer than petals; anthers ovate in outline, dorsifixed near base. Nectariferous disc fleshy, collar-like, with irregularly crenate margin, confluent with floral tube at base [or distinct to base], encircling the ovary. Stigmata 3, small, subcapitate, sometimes \pm confluent adaxially; style short, stout, 3-sulcate; ovary superior, 3-locular; ovules pleurotropous. Fruit a small, subglobular [to obovoid], purplish-black drupe with (2) 3 pyrenes; mesocarp fleshy [or leathery], thin; pyrenes thin-cartilaginous, dorsiventrally much compressed, obliquely obcordate, dehiscent along adaxial suture and upper half of the abaxial median.⁴ Seed rather flat, obliquely obcordate, slightly keeled submedially on ventral surface, orange-brown [or light brown], usually shining; seed coat thin, crustaceous; endosperm scanty; cotyledons suborbicular-obcordate, thin, the radicle minute. LECTOTYPE SPECIES: *S. theezans* (L.) Brongn.; see A. Rehder, Bibliogr. Cult. Trees Shrubs 436. 1949. (Named after Augustin Sageret, 1763–1851, French horticulturist and plant physiologist.)

A primarily tropical genus of nearly 30 species, centered in eastern Asia, extending south to Indonesia and northeastern Australia, west to southern Arabia and northeastern Africa; three species in North America, one occurring from Mexico south to Peru, Paraguay, and northern Argentina. *Sageretia minutiflora* (Michx.) Mohr,⁵ a trailing or straggling shrub usually six to ten feet tall, with polymorphic, relatively small leaves and very fragrant flowers, occurs on calcareous sandy soils, rocky bluffs, open dry copses, and margins of low rich woods (here sometimes ascending high

⁴The pyrenes of *Sageretia* have generally been described as indehiscent, but as early as 1907 Sprague stated that in at least *S. Brandrethiana* Aitch. the pyrenes are dehiscent. Recently, Grubov (Fl. USSR 14: 638. 1949) mentioned dehiscent pyrenes as a generic character in *Sageretia*, and Vikhireva (p. 258) described the dehiscence of pyrenes in *S. laetivirens* (Kom.) Gontsch. I have found the pyrenes dehiscent (when dried) in *S. minutiflora* and *S. elegans*, of the New World, and in *S. Henryi* Drumm. & Sprague, *S. lucida* Merr., and *S. spiciflora* (A. Rich.) Chiov. ex Hutch. & Bruce, of the Old World.

⁵*Sageretia minutiflora* (Michx.) Mohr, Contr. U. S. Natl. Herb. 6: 609. 1901. The authorship of this combination has usually been attributed to Trelease (1889, p. 367). However, Trelease's note under *S. Michauxii* Brongn., "If the specific name given by Michaux is to be retained, the plant becomes *S. minutiflora* (Michx.)," should be regarded as an incidental mentioning because Trelease himself did not adopt this name in either of his revisions of Rhamnaceae. Therefore, according to the International Code of Botanical Nomenclature (ed. 1961, Art. 34, Note 2) Trelease's mention of the combination does not constitute its valid publication.

trees) on the Coastal Plain from southern Florida (Lee County on the west and Brevard County on the east coast) to Mississippi and South Carolina. This species seems to be more closely related to the Mexican-South American *S. elegans* (HBK.) Brongn. and the wide-ranging Old World *S. theezans*, $2n = 24$, than to the Texan-Mexican *S. Wrightii* S. Wats.

The genus seems to be closely related to *Rhamnus*, combining in its fruits the dehiscent pyrenes of subg. RHAMNUS, the rather flat pyrenes and seeds of subg. PSEUDOFRANGULA, and the lateral raphe of subg. FRANGULA. It differs from *Rhamnus* especially in the nectariferous disc which is almost completely free from the floral tube.

The fruits of some species, e.g., *Sageretia theezans*, are said to be edible. Leaves of the same species are reportedly used as a substitute for tea in China.

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3. *Ceanothus* Linnaeus, Sp. Pl. 1: 195. 1753; Gen. Pl. ed. 5. 90. 1754.

Deciduous [to evergreen] unarmed [or spinescent] shrubs [rarely small trees], with 3-lacunar nodes. Leaves alternate [or opposite], membranaceous [or coriaceous], serrulate or crenate-serrulate to subentire [or serrate, or spinulose], 3-nerved at base [or pinnately veined]; stipules small, thin, deciduous [or \pm corky, persistent]. Inflorescences terminal and/or axillary, peduncled, raceme- or corymb-like thyrses composed of few-flowered umbel-like cymes, or the flowers solitary or in few-flowered cymes in the leaf axils at the top of leafy branchlets. Flowers small, usually 5-merous [exceptionally 6-8-merous], perigynous, bisexual, white [blue to lavender], slender pediceled, the calyx and pedicels colored like the petals. Floral tube shallow, cupular-turbinate to hemispherical; calyx lobes triangular, petaloid, usually \pm inflexed, deciduous. Petals hooded, clawed, longer than calyx lobes, \pm spreading, inserted at base of disc. Stamens exserted, equalling or exceeding petals; anthers ovate-cordate in outline. Nectariferous disc annular, tumid, often distinctive in color, encircling the upper portion of the ovary. Stigmata 3, small, subcapitate; style 3-forked in the upper third to half; ovary semi-inferior, 3-locular, incompletely so at the very base; ovule pleurotropic. Fruit a small purplish-black drupe, \pm 3-lobed or -cornered, smooth or crested [ridged or horned] on back of lobes or corners at their tops, supported by and adnate to the persistent base of floral tube, containing 3 coherent pyrenes; mesocarp thin, fleshy or \pm leathery; pyrenes cartilaginous, obovate in

outline, convex on abaxial, angular on adaxial surface, explosively dehiscent along adaxial suture and upper portion of the abaxial median, ejecting seeds. Seed narrowly to broadly obovoid, plano-convex, dark brown to black, smooth, shining, with a lateral raphe, minutely arillate at base; seed coat crustaceous; endosperm fleshy, scarce; embryo large, the cotyledons broadly elliptic- to suborbicular-cordate, flat, thin, the radicle minute. TYPE SPECIES: *C. americanus* L.; typified by the removal of two of the three original species to other genera; see A. Brongniart, Mém. Fam. Rhamn. 62, 64. 1826. (Name from Greek, *keanothos*, the name of some prickly plant mentioned by Theophrastus, applied to this genus by Linnaeus.) — REDROOT.

An exclusively American genus of nearly 55 species, distributed from Guatemala (one species) north to southern Canada, centered in California (44 species). Two natural, very distinct sections, CEANOTHUS, with ca. 36 species, and CERASTES S. Wats., with 19 species, are recognized. Four species of sect. CEANOTHUS occur in our area.

Ceanothus americanus L., New Jersey tea, $2n = 24$, a low shrub or subshrub up to a meter tall, with mostly ovate leaves and axillary, mostly raceme-like thyrses on elongated leafless peduncles, occurs in woods, hill-sides, ravines, and prairies from southern Quebec and southern Ontario west to Minnesota and Nebraska, south to Texas and northern Florida. Its slender-branched variant with leaves usually 2–4 cm. long (in Gleason's delimitation), known as var. *intermedius* (Pursh) Torr. & Gray,⁶ seems to represent the species on the sterile or sandy ground of the Coastal Plain, from Massachusetts south to central Florida and west to Louisiana and Arkansas. Another variant, var. *Pitcheri* Torr. & Gray, with lower leaf surface densely permanently velutinous, occurs scattered throughout the range of the species, but appears to be predominant in the prairies from Illinois west and southwest. Dried leaves of this species were used as a substitute for tea during the American Revolution. *Ceanothus serpyllifolius* Nutt., a low, diffusely branched shrub 20–45 cm. tall, with ovate-elliptic leaves 0.6–1.25 cm. long and axillary, few-flowered, corymb-like thyrses on elongated leafless peduncles, occurs in a few scattered localities in pine-lands on the Coastal Plain of Georgia and Florida, south to Volusia County. It is "closely allied to *C. americanus* var. *intermedius*, from which it differs chiefly in size" (Trelease, 1897, p. 410). The specific status of this plant is questionable.

Ceanothus herbaceus Raf. (*C. ovatus* Desf.), a shrub up to 1 m. tall, with oblong-elliptic to elliptic-lanceolate leaves and terminal, short-

⁶ This variant has been variously delimited with regard to the leaf size: e.g., leaves mostly under 1 inch long (Trelease, 1888, 1897; McMinn in Van Rensselaer & McMinn); 2–4 cm. long (Gleason, New Britt. Brown Illus. Fl. NE. U. S. 2: 514. 1952); or 2–6 cm. long (Fernald, Gray's Man. Bot. ed. 8. 993. 1950). Such different delimitations produce rather different ranges for this variety. Until extensive population studies are made and the results carefully evaluated, the limits of this variant, the existence of a distinct range, and, consequently, its varietal status will remain uncertain.

peduncled, corymb-like thyrses, occurs in upland and rocky prairies, rocky woodland, open rocky places, calcareous bluffs, and dry ground, from southern Quebec to southern Manitoba, North Dakota, and Colorado, south to Nebraska, Kansas, Oklahoma, and Texas (locally in Eddy County, in southernmost New Mexico), Arkansas, locally in central Tennessee (White County), Kentucky, West Virginia, northernmost Virginia (Arlington County), the District of Columbia, and New Jersey, and, according to McMinn, in Lake County, Florida (the specimen *Nash 1041* not seen by the writer). A variant with the lower surface of the leaves permanently densely villous, has been regarded as *C. herbaceus* Raf. var. *pubescens* (S. Wats.) Shinnars (*C. ovatus* var. *pubescens* S. Wats.), but Soper showed that this variant, "which has generally been considered as having a more western distribution, occurs within the range of the species even as far east as the Great Lakes and northeastern Massachusetts, and therefore should be considered "as merely a pubescent form."

Ceanothus microphyllus Michx., a low, diffuse shrub or subshrub 15–60 cm. tall, with leaves 3–7 mm. long, alternate and often also fasciculate in the leaf axils, and small terminal corymb- or raceme-like panicles, occurs in dry pine- or oak-woods on the Coastal Plain from Highlands County, Florida, to southwestern Alabama and southern Georgia. The terminal inflorescences suggest a close relationship to *C. herbaceus*.

The flowers of *Ceanothus* usually are 5-merous and the floral anatomy very uniform, although 6–8-merous flowers with an additional vascular bundle to each extra floral segment occur regularly in *C. Jepsonii*.

The genus is homoploid, the chromosome number being invariably $2n = 24$ in the 34 species investigated (Nobs); the karyotype is also uniform. Intersectional hybrids are extremely rare and always sterile, indicating a strong genetic barrier between the sections. On the contrary, intrasectional interspecific hybrids, both natural and artificial, are very numerous.

The roots of some species (e.g., *Ceanothus americanus*, *C. velutinus* Dougl.) are known to develop mycorrhizal nodules in great abundance. The presence of nitrogen-fixing bacteria in these nodules seems to be questionable (cf. Furman).

The fossil records indicate that *Ceanothus* has been present on the Pacific slope of North America at least since the Oligocene and that the differentiation of the two sections of the genus might already have occurred in the Miocene (cf. Nobs, p. 78).

The genus seems to be closely related to *Colubrina* Brongn.

Numerous species and hybrids of *Ceanothus* are valuable ornamentals. *Ceanothus americanus*, *C. ovatus*, and *C. coeruleus* Lag. (*C. azureus* Desf.), the earliest species introduced into cultivation, provided the basis for many attractive garden hybrids. Many species are important as sources of food and shelter for wildlife; some can also be used for erosion control.

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4. **Colubrina** L. C. Richard ex Brongniart, Mém. Fam. Rhamn. 61. 1826, nom. cons.

Unarmed or spinescent evergreen shrubs or small [very rarely large] trees. Leaves alternate [rarely opposite], membranaceous to subcoriaceous [or coriaceous], pinnately nerved or 3-nerved from base, entire or finely [to coarsely] toothed, often with small, round glands scattered on lower surface and/or 1 or 2 glands at base of blade; stipules minute, free, caducous [or connate in the axil, persistent]. Inflorescences axillary cymes or small thyrses, sessile and umbel-like or short peduncled, few flowered, and corymb-like [or flowers rarely axillary, solitary]. Flowers small, usually 5-merous, bisexual, perigynous. Floral tube hemispherical: calyx lobes triangular-ovate, spreading, conspicuously keeled on inner surface, deciduous. Petals greenish yellow to yellow or white, cucullate, sessile to short-unguiculate, shorter than calyx lobes, inserted at exterior margin of disc. Stamens nearly as long as petals; anthers ovate in outline, subbasifixed, introrse. Nectariferous disc large, fleshy, pentagonal or indistinctly shallowly 10-lobed, filling the floral tube, surrounding the ovary and adnate to its lower half. Stigmata 3, small, obtuse; style slender, 3-lobed to -fid; ovary semi-inferior, 3-locular; ovules pleurotropic. Fruit a subglobular, \pm 3-lobed orange-red to black drupe supported at the base by the adnate floral tube; mesocarp thin and dry [or \pm fleshy]; stone cartilaginous or crustaceous, 3-locular, splitting septicidally into 3 pyrene-like carpels dehiscent along the whole adaxial suture and halfway down abaxially. Seeds broadly obovate in outline, convex on abaxial, flattish-angular on adaxial side, brown to black, usually lustrous, smooth or sometimes pitted, sometimes with a minute aril at base; seed coat coriaceous to almost bony; endosperm fleshy, thick; embryo straight, axial, the cotyledons flat, \pm fleshy, elliptic-suborbicular, the radicle small. (Including *Cormonema* Reissek ex Endl., and *Hybosperma* Urb.) LECTOTYPE SPECIES: *C. ferruginosa* Brongn. = *C. arborescens* (Mill.) Sarg.; see N. L. Britton, N. Am. Trees 681. 1908. (Name apparently derived from *bois couleuvre*, snakewood or serpent tree, the French name of the type species on Martinique, translated into Latin as *Arbor colubrina* by Jacquin, Select. Stirp. Am. Hist. 75. 1763.)

An almost pantropical genus of nearly 30 species, centered in tropical America, with a few species in southeastern Asia, Malesia, tropical Australia and Polynesia (to Hawaii), with one species in coastal East Africa and the Mascarene Islands; three indigenous and one naturalized species in our area. The genus has recently been subdivided into subg. COLUBRINA, with entire, pinnately veined leaves, and subg. SERRATARIA M. C. Johnst., with glandular-serrate leaves often 3-nerved at base. Each subgenus comprises two sections.

Subgenus COLUBRINA sect. COLUBRINA, with branchlets not spinescent, glands scattered on the lower leaf surface, and pyrene-like parts of the stone dehiscing explosively, includes about five tropical American species. *Colubrina arborescens* (*C. ferruginosa*, *C. Colubrina* (Jacq.) Millsp.), wild-coffee, a shrub or small tree with rusty tomentose branchlets, ovate to elliptic leaves 5–15 cm. long, and stout-pedicelled drupes, known from the West Indies and Mexico to Guatemala, occurs in the hammocks of southernmost peninsular Florida and on the Florida Keys. Section VELLOZIA M. C. Johnst., with branchlets spinescent, leaf blades biglandular near the base, and dehiscence of the fruits not explosive, includes seven species, all tropical American. *Colubrina elliptica* (Sw.) Brizicky & Stern (*C. reclinata* (L'Hér.) Brongn.), soldierwood or nakedwood, a shrub or small tree with puberulent branchlets, ovate-elliptic to elliptic or obovate leaves, and slender-pedicelled drupes, of the West Indies and Mexico to Venezuela, occurs in southernmost peninsular Florida (Dade County) and on the Florida Keys. This species "seems to be intermediate between the two sections and to link them together" (Johnston, p. 91).

Subgenus SERRATARIA M. C. Johnst. sect. SERRATARIA, with leaves more or less evenly pinnately veined [or 3-nerved at base] and fruits thick walled and tardily dehiscent, is a primarily West Indian-Mexican group of nine species, extending north to California, southern Arizona, Texas, and southernmost Florida. The West Indian *Colubrina cubensis* (Jacq.) Brongn. is represented in hammocks of southern peninsular Florida by var. *floridana* M. C. Johnst., a shrub or tree with leaves narrowly elliptic-oblong to lance-oblong, 5–10 cm. long and 1.2–3.8 cm. broad, finely tomentose on both surfaces, rounded or obtuse at apex, rounded or broad-cuneate at base, with obscurely crenulate-serrulate, somewhat revolute margins. Section BARCENA (Duges) M. C. Johnst., including two Mexican and five Old World species, is represented in the coastal hammocks of southernmost peninsular Florida (north to Palm Beach County) and on the Florida Keys by the naturalized *C. asiatica* (L.) Brongn., a glabrous shrub with weak diffuse or prostrate branches (rarely erect and treelike) with ovate, finely crenate-serrulate leaves 3-nerved at base. The species is widely distributed in the tropics of the Old World, in Asia, Malesia, the Pacific islands, tropical Australia, the Mascarene Islands, and coastal East Africa, and is naturalized in tropical continental America and the West Indies. Seeds of this species float and are distributed by sea currents.

The genus is closely related to *Ceanothus*.

The close-grained, hard and heavy wood of some species (e.g., *C. arborescens*, *C. elliptica*) is of some local importance.

REFERENCES:

Under family references see GEMOLL (pp. 380–382), SARGENT (pp. 729–731), SUESSENGUTH (pp. 85–89), TRELEASE (1897, p. 418), VIKHIREVA (1952, pp. 265, 266), and WEST & ARNOLD (pp. 136, 137).

BRIZICKY, G. K., & W. L. STERN. Notes from the S. J. Record Memorial Collection. II. Trop. Woods 109: 95, 96. 1958. [*C. elliptica* the correct name instead of *C. reclinata*.]

JOHNSTON, M. C. Novelties in *Colubrina* including *Cormonema* and *Hybosperma* (Rhamnaceae). *Wrightia* 3: 91, 92. 1963; 93–96. 1964.

SARGENT, C. S. *Colubrina*. *Silva N. Am.* 2: 47–50. *pl.* 66. 1891.

Tribe PALIUREAE Reisseck⁷

5. **Berchemia** Necker ex De Candolle, *Prodr.* 2: 22. 1825, nom. cons. prop.

Glabrous, deciduous, twining woody vines [or shrubs to small trees]. Leaves alternate, membranaceous, pinnately veined, with 9–12 pairs of slightly curved, subparallel primary veins, entire, often wavy. Inflorescences raceme-like thyrses composed of few-flowered, peduncled to sessile corymb-like terminal cymes (sometimes also occurring in the axils of a few leaves just below the thyrses). Flowers small, 5-merous, perigynous, unisexual by abortion [or bisexual?], the plants apparently dioecious. Floral tube saucer- to shallowly cup-shaped; calyx lobes considerably longer than floral tube. Petals greenish white, obovate or oblanceolate, somewhat concave, \pm acute at apex, not clawed in δ , often very shortly clawed in ♀ flowers, nearly as long as [or somewhat shorter than] calyx lobes, inserted at the exterior margin of the disc. Stamens longer than petals in δ , shorter and sterile in ♀ flowers; anthers ovate in outline, slightly cordate, dorsifixed near base. Nectariferous disc fleshy, filling floral tube, pentagonal, broad and flat in δ , narrow with somewhat raised interior margin and encircling ovary base in ♀ flowers. Gynoecium rudimentary in δ flowers; stigmata 2, small, subcapitate-discoid; style narrowly conical, usually short-bifurcate; ovary superior, 2-locular, the 2 septa distinct, overlapping each other and extending to opposite ovary wall, accumbent; ovules probably at first epitropous, later changing to pleurotropous during development. Fruit a small, bluish-black, ellipsoid to narrowly obovoid, apiculate single-stoned drupe, supported at base by remnant of floral tube; mesocarp fleshy, often juiceless, thin; stone 2-

⁷ The tribe Paliureae Reisseck in Endlicher (*Gen. Pl.* 1095. 1840) was originally composed of two genera, *Paliurus* Mill. and *Ventilago* Gaertn. In 1862, Bentham and Hooker (*Gen. Pl.* 1: 372) established the tribe Ventilagineae to include *Ventilago* and *Smythea* Seem. and placed *Paliurus* in the new tribe Zizipheae. Inclusion of *Paliurus*, the type genus of the tribe Paliureae, in Zizipheae by Bentham and Hooker makes the latter name illegitimate. The correct name for this tribe is Paliureae, and the tribe is to be taxonomically emended to include all the genera of Zizipheae.

locular, bony, thickish, 1- or 2-seeded, indehiscent. Seed subcylindric-ovoid; seed coat membranaceous, thin, adherent and partly adnate to endocarp; endosperm fleshy, scarce; cotyledons oblong, plane, parallel with partition, the radicle short, slightly curved. (*Oenoplea* (Pers.) Michx. ex Hedw. f., nom. rejic. prop.; see *Taxon* 12: 170. 1963.) TYPE SPECIES: *B. volubilis* (L. f.) DC. = *B. scandens* (Hill) K. Koch. (Name said to commemorate either Nikolaus Berghem, alias Berchem, 1624–1683, a Dutch landscape, plant, and animal painter, or Berthout van Berchem, a contemporary of Necker.)⁸

A primarily tropical genus of 22 (or fewer) species, all except one of Asia (Japan to Afghanistan, south to Java, Celebes, and Timor). The single American species, *Berchemia scandens*, supple-jack or rattan vine, occurs in hammocks, in rich or low woods, or in swamps from southernmost peninsular Florida west to Texas, north and northeast to Arkansas, southern Missouri, Tennessee, and Virginia; disjunct in southern Mexico (Chiapas) and Guatemala (Baja Verapaz). It is "one of the many vines which semi-strangle trees; the tree trunks sometimes nearly grow over this vine, thus producing an ill-shaped non-merchantable trunk" (Brown).

The genus seems to be more or less closely related to *Rhamnella* Miq., *Berchemiella* Nakai, and *Chayadaia* Pitard, all small genera of the Old World. The primarily East African *Phyllogeiton* (Weberb.) Herzog, comprising two species, has sometimes been included in *Berchemia*, but such a close relationship has not been convincingly demonstrated.

A few Asiatic species are sometimes grown as ornamentals. A basic, karyophilic stain, berchemine, was recently obtained from the crushed berries of *Berchemia lineata* (L.) DC.

REFERENCES:

- Under family references see BROWN (pp. 178, 179), HERZOG (pp. 166–168), SUESSENGUTH (pp. 141–145), TRELEASE (1897, pp. 404, 405), and VIKHIREVA (1952, p. 259).
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⁸There were, however, two of Necker's contemporaries with the same name: Berthout van Berchem, *père*, and Berthout van Berchem, *filis*, both active members of the Society of Natural History in Lausanne, Switzerland. The father was the author of a few articles on agriculture (e.g., on cultivation of potatoes and on soils); the son seems to have been a more prominent zoologist (mammalogist) and chemist.

6. *Ziziphus* Miller, Gard. Dict. Abr. ed. 4. 1754.

Deciduous [or evergreen] shrubs or small trees [rarely woody vines], armed with often unequal stipular spines [or \pm axillary solitary or paired thorns, or rarely unarmed]; a few deciduous branchlets resembling pinnate leaves often fascicled in the leaf axils. Leaves alternate [rarely subopposite to opposite, or fascicled], 3-nerved to or almost to the apex [or only at base, or pinnately nerved throughout], crenate-serrulate [to crenate-serrate or entire]; stipules modified to spines [or minute, caducous]. Inflorescences axillary, few-flowered, subsessile to sessile [peduncled], corymb-like cymes [or terminal or axillary thyrses]. Flowers small, usually 5-merous, perigynous but appearing subepigynous, bisexual, usually yellow. Floral tube shallow, subpatelliform [to hemispherical]; calyx lobes keeled medially and swollen at apex within, deciduous. Petals hooded, unguiculate, shorter than the calyx lobes [rarely wanting]. Stamens somewhat longer than petals; anthers introrse [rarely extrorse], ovate to elliptic in outline. Nectariferous disc fleshy, \pm flat, \pm pentagonal [or \pm 10-lobed], surrounding ovary and \pm adherent to it. Stigmata 2 [3], small, subcapitate-discoïd; style 2[3]-furcate, swollen toward base into a stylopodium separated from ovary by a shallow groovelike constriction; ovary appearing to be inferior or semi-inferior (becoming superior in fruit), immersed to the stylopodium in the disc, 2[3]-locular [or incompletely so], the septa meeting in the center, connate [or distinct]; ovules pleurotropic, basal (Prichard) or subbasal (Nair & Sarma). Fruit an ellipsoid, ovoid to slightly obovoid [or subglobular], dark-red to black single-stoned drupe, 1.5–3[–5] cm. long; mesocarp fleshy; stone bony, ovoid to narrowly ellipsoid, sharply pointed at apex or at both ends, smooth or furrowed, 2[3]- or 1-locular by abortion, 1-seeded, indehiscent. Seed elliptic in outline, nearly plano-convex, the raphe lateral; seed coat thin, membranaceous; endosperm fleshy, scanty; embryo straight, the cotyledons large, thick, plane, the radicle small. LECTOTYPE SPECIES: *Rhamnus Ziziphus* L. = *Z. Jujuba* Mill.; see Britton & Wilson, Sci. Surv. Porto Rico Virgin Is. 5(1): 535. 1923. (Latin name of the type species, first introduced by Pliny; etymology obscure.)⁹

A pantropical genus of nearly 100 species, extending locally into the Temperate Zone; centered in southeastern Asia and in tropical America, where the genus ranges from southern Brazil, Paraguay, northern Argentina, and Peru north to the West Indies, Mexico, and the southwestern United States. Although the species of the New World form a group rather distinct from those of the Old (Johnston), no subgeneric categories have

⁹ The name has been designated by various authors as being derived from Old Phoenician, *zizuf*; Arabic, *zezaf* or *zefzaf*; Persian, *zizafun*; and Greek, *ziziphos*. According to Löw (Fl. Juden 3: 139. 1924) the plant, which was first introduced into Rome from Syria by the end of the reign of the Emperor Augustus, in the first century A.D., brought its name *ziziphus* from there. This name was further introduced into some European and Oriental languages from Hebrew, from which the Greek word *zizyphos* was also derived.

been established yet. The Old World group is represented in our area by the cultivated and naturalized *Ziziphus Jujuba* Mill. (*Z. Ziziphus* (L.) Karst.), Chinese or common jujube, $2n = 24, 26, 40, 48, 74, 96$, occurring rarely in thickets and on roadsides on the Coastal Plain from Alabama to Louisiana. *Ziziphus mauritiana* Lam. (*Z. Jujuba* Lam., not Mill.), Indian jujube, $2n = 48$, differing in the leaves densely tomentose beneath, is also cultivated in the southern part of our area for its edible fruits.

Bees are regarded as common pollinators, and cross-pollination seems to be the rule. Although self-pollination and -fertilization sometimes occur, the fruits in such cases are small and tend to drop off prematurely. Parthenocarpy and (rarely) polyembryony have been recorded in *Z. Jujuba*.

The genus seems to be closely related to the Asiatic-South European *Paliurus* Mill.

Some species, especially the two above, are widely cultivated as fruit trees. The wood of some is of local importance.

REFERENCES:

- Under family references see BROWN (p. 179), HERZOG (pp. 127-147), MIERS, NAIR & SARMA, PRICHARD (pp. 85-88), SUESSENGUTH (pp. 123-132), and VIKHIREVA (1952, pp. 269-273).
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7. *Reynosia* Grisebach, Catal. Pl. Cubens. 33. 1866; emend. Urban, Symb. Antill. 9: 225. 1924.

Evergreen shrubs or trees. Leaves usually opposite or subopposite [rarely partly alternate], coriaceous, entire, pinnately veined, with 6–15 pairs of inconspicuous primary veins and numerous finely reticulate veinlets visible only with magnification; stipules connate laterally at least half their length in the axil, persistent. Inflorescences axillary sessile, subumbellate, cymose fascicles, sometimes reduced to solitary flowers. Flowers small, yellowish green, 5-merous, perigynous, bisexual, pediceled. Floral tube short-campanulate to hemispherical; calyx lobes ovate, acute, spreading, deciduous. Petals wanting [or present]. Stamens shorter than calyx lobes, inserted on upper margin of disc; anthers elliptic in outline, dorsifixed near base, slightly versatile. Nectariferous disc fleshy, lining floral tube. Stigmata 2; style short, stout, 2-lobed; ovary superior, 2-locular, the 2 septa meeting in the center or overlapping each other and extending nearly to the opposite ovary wall, accumbent, but distinct; ovules pleurotropic. Fruit a small, subglobular to ellipsoid, purple to black, single-stoned drupe; mesocarp fleshy, thin; stone thickish, \pm bony, ellipsoid-subglobular, usually 1-locular by reduction of the second locule, indehiscent. Seed ovoid to subglobular; seed coat membranaceous, thin, rugose, adherent to the endocarp; endosperm copious, hard, ruminant; embryo relatively small, the cotyledons oblong or elliptic, flat, the radicle elongate. LECTOTYPE SPECIES: *R. retusa* Griseb.; see N. L. Britton, N. Am. Trees 673. 1908. (Named after Alvaro Reynoso, 1830–1888, Cuban agriculturist and chemist.)

A West Indian genus of about 16 species. Subgenus *NEOREYNOSIA* Suesseng. includes nine species with petaliferous flowers, while subg. *REYNOSIA* includes seven, one in our area, all with apetalous flowers. *Reynosia septentrionalis* Urb., darling plum, red ironwood, a shrub or small tree of Cuba and the Bahamas, occurs in hammocks on the Florida Keys and in peninsular Florida ("north on east coast to central Florida," according to Little, U. S. Dep. Agr. Handb. 41: 361. 1953). Fruits of this species are edible and are said to be pleasantly flavored.

Despite its ruminant endosperm, the genus seems to be closely related to the West Indian *Krugiodendron* and *Doerpfeldia* Urb., on the one hand, and to *Berchemia* and its allies, on the other.

The close-grained, very hard and heavy wood of a few species (e.g., *R. septentrionalis*, *R. guama* Urb., *R. regia* Urb. & Ekm.) seems to be of some local importance.

REFERENCES:

Under family references see HERZOG (pp. 154–158), SARGENT (pp. 720, 721), SUESSENGUTH (pp. 136–138), VIKHIREVA (1952, pp. 260, 261), URBAN, and WEST & ARNOLD (p. 138).

SARGENT, C. S. *Reynosia*. Silva N. Am. 2: 19–22. pl. 56. 1891.

8. **Krugiodendron** Urban, Symb. Antill. 3: 313. 1902.

Evergreen trees or shrubs. Leaves opposite or subopposite, thin and firm to coriaceous, entire, pinnately veined, with 4–6 pairs of slightly curved primary veins and coarsely reticulate veinlets \pm prominent on the upper surface; petioles short, stout; stipules small, connate laterally at the very base in the axil, persistent. Inflorescences axillary, few-flowered, shortly peduncled to sessile, umbel-like cymes. Flowers 5-merous, small, greenish yellow, bisexual, pediceled. Floral tube broadly obconical, rather flat; calyx lobes triangular, acute, conspicuously crested on inner surface, erect or spreading, deciduous. Petals wanting. Stamens inserted under margin of disc, shorter than sepals, suberect in aestivation; anthers ovate to ovate-suborbicular in outline, obtuse. Nectariferous disc fleshy, broad-annular, \pm 5-lobed, surrounding base of ovary. Stigmata 2, small; style short, stout, 2-lobed to -fid; ovary superior, 2-locular, the 2 septa overlapping each other, extending to the opposite ovary wall, accumbent, distinct; ovules pleurotropic. Fruit an ovoid to ovoid-subglobular, black, single-stoned drupe; mesocarp fleshy, thin; stone bony, 2-locular (one locule often \pm reduced), 1(2)-seeded, indehiscent. Seed ellipsoid, \pm compressed dorsiventrally; seed coat membranaceous, adherent to the endocarp; endosperm wanting; embryo large, the cotyledons elliptic to subobovate, plano-convex, the radicle minute, retracted between the cotyledons. TYPE SPECIES: *K. ferreum* (Vahl) Urb. (Named in honor of Leopold Krug, 1833–1898, German botanist, explorer of the West Indian flora.)

The single species, *Krugiodendron ferreum* (*Rhamnidium ferreum* (Vahl) Sarg.), black ironwood, of the West Indies and Central America (Guatemala to southern Mexico), occurs in hammocks on the Florida Keys and in peninsular Florida from Monroe and Dade counties north to Cape Canaveral (Cape Kennedy), Brevard County. The species is closely related to and perhaps congeneric with the monotypic Cuban genus *Doerpfeldia* Urb., which seems to differ from *Krugiodendron* mainly in the alternate leaves. The close-grained, hard wood is the heaviest occurring in the United States (specific gravity 1.3–1.4).

REFERENCES:

Under family references see HERZOG (pp. 153, 154), SARGENT (pp. 721, 722), and SUESSENGUTH (p. 147), and WEST & ARNOLD (p. 138).

SARGENT, C. S. *Rhamnidium*. *Silva N. Am.* 2: 27–30. *pl.* 58. 1891.

Tribe GOUANIEAE Reisseck

9. **Gouania** Jacquin, Select. Stirp. Am. Hist. 263. 1763.

Deciduous vines climbing by solitary tendrils located at apex of short sterile axillary shoots or laterally near the bases of inflorescences. Leaves alternate, membranaceous to subcoriaceous, pinnately veined, sometimes

± distinctly 3-nerved at base, with 4–7 pairs of ascendent curved primary veins, coarsely and ± remotely crenate-serrate, each tooth usually with a small patelliform gland. Inflorescences axillary and terminal spike- or raceme-like thyrses composed of glomerules. Flowers small, 5-merous, epigynous, bisexual [or more commonly bi- and unisexual], short pedicel to subsessile. Floral tube broadly obconical to subcampanulate; calyx lobes persistent. Petals whitish or greenish white, ovate, concave, short clawed, inserted under the margin of the disc in its sinuses. Nectariferous disc epigynous, fleshy, 5-lobed [or pentagonal]; each lobe (opposite a sepal) extended into a distinct short and rounded or apically bilobed [or elongated and acuminate] staminode-like structure. Stigmata 3, small; style 3-lobed to -furcate; ovary inferior, 3-locular; ovule pleurotropic. Fruit a 3-locular schizocarp with 3 rounded commissural wings [or rarely unwinged], splitting septicidally through each wing into three 2-winged indehiscent mericarps separating from a 6-parted carpophore. Seed obovate in outline, convex abaxially, somewhat angular adaxially, or lenticular; seed coat bony, shining; endosperm scarce; cotyledons roundish, plane, the radicle very short. LECTOTYPE SPECIES: *G. tomentosa* Jacq. = *G. polygama* (Jacq.) Urb.; see Britton & Millspaugh, Bahama Fl. 258. 1920. (Named after Antoine Gouan, 1733–1821, physician and botanist, author of the *Hortus Regius Monspeliensis*, 1762, and *Flora Monspeliensis*, 1765.)

A pantropical genus of nearly 50 species, about 20 in tropical America, extending north to Mexico, the West Indies, and Florida; an almost equal number in southeastern Asia, eastern Australia, New Caledonia, and Polynesia; and the remainder in Africa, Madagascar, and the Mascarene Islands.

Gouania lupuloides (L.) Urb., chewstick, with the range of the genus in America, occurs in hammocks on the Florida Keys and in southern peninsular Florida, north to Brevard and Manatee counties. In the West Indies, pieces of the stem are chewed to heal and harden the gums and to cleanse the teeth. The dried and powdered stems are used in making dentifrices.

The genus seems to be closely allied to *Reissekia* Endl. of Brazil, and to the East Indian-East African *Helinus* E. Mey. ex Endl. It also shows somewhat more remote relationships to *Ceanothus* and *Colubrina*.

REFERENCES:

Under family references see GEMOLL (pp. 412–420), PRICHARD (pp. 97, 98), SUESSENGUTH (pp. 166–171), TRELEASE (1897, p. 419), and VIKHIREVA (1952, pp. 280, 281).

TROLL, W. Vergleichende Morphologie der höheren Pflanzen. Band 1 (Teil 1). i–xii + 955 pp. 1935–1937. [*Gouania*, tendrils modified axillary shoots, 851.]